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Load-lifting Constraints on Provisioning and Nest Building in the Carpenter Wasp, *Monobia quadridens* L. (Hymenoptera: Eumenidae)

PAULA K. EDGAR AND JOSEPH R. COELHO

(PKE) Department of Instructional Services, John Wood Community College, 150 South 48th Street, Quincy, Illinois 62301, USA; (JRC) Department of Biology, Culver-Stockton College, One College Hill, Canton, Missouri 63435, USA

Abstract.—The foraging and mud-carrying capacity of the trap-nesting carpenter wasp, *Monobia quadridens* L., was examined in relation to load-lifting ability. The body mass of caterpillar prey collected increased over the course of the season. Consequently, the ability of the wasps to carry prey became compromised late in the season. Caterpillar mass was not correlated with wasp size, but the mass of mudballs used in nest construction was related to wasp size. Wasp foraging may be constrained by the size of pyralid caterpillars available at any particular time, which changes because of caterpillar growth. Mudballs are constructed by the wasps themselves; therefore, wasps may be able to optimize mudball size in accordance with their own size, but mudballs were much lighter than caterpillars and never approached the upper limit of the wasps' ability to carry them.

Optimal foraging theory suggests that an animal will experience increased fitness as it becomes more efficient at obtaining food or energy. One obstacle encountered by flying insects that carry food loads is the need to generate sufficient lift force to remain airborne. Prey selection may be limited by the size of the prey the insect can successfully carry while in flight. Marden (1987) demonstrated that maximum still-air lift force in flying animals depends primarily on flight muscle mass (M_{fm}). A fixed minimum ratio of flight muscle mass to total mass lifted, the marginal flight muscle ratio, is required for successful takeoff. Animals with higher flight muscle ratios (FMR) have greater maneuverability, and should be better able to lift and carry loads, seize prey, avoid predators and vie for territories and mates (Marden 1987).

Recent studies examining the relationship between maximum lift force and actual load carriage in foraging and provisioning wasps have used ground-nesting species, including *Vespula* spp. (Coelho and Hoagland 1995), *Sphecius speciosus* Drury (Coelho 1997), and *Sphex ichneumoneus* L. (Coelho and LaDage 1999). In the present study we investigate load carriage during provisioning and mud-carrying in *Monobia quadridens* L. (Hymenoptera: Eumenidae), an aerial nester.

Aerial nesting may apply additional constraints to load carriage. Two ground nesting species, the cicada killer (*Sphecius speciosus*) and the great golden digger wasp (*Sphex ichneumoneus*) are able to carry heavier loads than are theoretically possible, primarily by climbing vegetation, then flying toward their burrows (Coelho 1997, Coelho and LaDage 1999). Although presumably using maximum power, such overloaded wasps can only descend. Aerial nesters lack this option, as the final flight to the nest requires a vertical takeoff and ascent to the nest entrance. *M. quadridens* may not attempt to carry near-maximal loads if the load compromises flight maneuverability and nest entry.

The carpenter wasp, *M. quadridens*, readily nests in old borings of carpenter bees, *Xylocopa* spp. (Tandy 1908, Rau 1935), and is the largest vespoid wasp to use wood trap-nests (Krombein 1967). A mature female removes debris inside the nest cavity and collects mudballs by moistening soil with water stored in the wasp's crop (Spradbery 1973) or with saliva (Evans and Eberhard 1970). Mudballs are used to construct the nest's interior plug, cellular partitions and exterior plug. Prior to mass provisioning with paralyzed caterpillar prey, a female deposits an egg near the inner end of the cell (Krombein 1967, Spradbery 1973). A partition is constructed between cells. A vacant space, the vestibular cell, is made near the nest's opening and sealed with a thick exterior plug. *Monobia quadridens* takes four to seven days to provision a nest (Krombein 1967).

The larva emerges 5 to 8 days after the egg is laid, feeds on the paralyzed caterpillars, applies a varnish to the cell's interior and pupates. The elapsed time between pupation and adult emergence averages 17 days for males and 18 days for females (Krombein 1967). Teneral adults remain inside their cells for 2 to 3 days while their integument and wings sclerotize, then chew through the cell partition to escape from the nest (Krombein 1967, Cowan 1991).

Monobia quadridens often provisions its nest with a single species of Lepidoptera; with pyralid caterpillars the most frequent. Stenomid and tortricid caterpillars were also used to provision nests (Krombein 1967). Female *M. quadridens* collecting long caterpillars, 10–18 mm, used fewer caterpillars per cell than those using prey that were only 6–13 mm in length (Krombein 1967). Theoretically, wasps carrying larger loads make fewer trips, thus conserving time and energy (Reavey 1993). The demands of temporal and energetic efficiency therefore interact with the constraints of load-lifting.

This study examines how load-lifting limitations influence the provisioning and mud-carrying strategies of *M. quadridens*. A female wasp should carry caterpillars and mudballs that are near the maximum load-lifting capacity without exceeding it in order to save time and energy by reducing the number of trips. In other words, a female carrying prey or mudballs should have a FMR slightly above the marginal FMR for Hymenoptera, 0.179 (Marden 1987).

MATERIALS AND METHODS

Field research was conducted from June through September 1996, 1997 and 1998 at Alice L. Kibbe Life Science Station, Hancock County, Illinois. Observations and data collection were limited to sunny days because *M. quadridens* was not very active on overcast or rainy days.

M. quadridens females were nesting in abandoned carpenter bee holes in the wooden support beams beneath the upper level porch on the east side of the Frank House, a wooden frame building housing the field station's education center. To provide additional nesting sites for *M. quadridens*, artificial trap-nests were constructed according to Krombein (1967). A 12.7-mm diameter hole was drilled along the central longitudinal axis of straight-grain pine boards (38.1 mm × 38.1 mm × 200 mm) to a depth of approximately 152 mm. 12.7 mm dia holes adequately accommodate *M. quadridens* females' large size (Krombein 1967). Metal brackets held the traps in place on the faces of the support beams at two meters.

Initially, female wasps without prey were captured with an insect net and coaxed individually into a 1.5 ml microcentrifuge tube (ventilated by puncturing a hole in the lid) and placed in the refrigerator for 30 minutes. Wasps were marked on the dorsal side of the thorax with one or two small dots of enamel hobby paint. Special care was taken to avoid getting paint on antennae, wings or spiracles. Body mass (M_b) for each wasp was determined to the nearest 0.001 g on an Ohaus® electronic balance. The wasp was then placed outdoors near the nesting site and allowed to recover fully and fly away. Individuals recaptured over the course of several days had M_b measured for each of those days.

Subsequent captures of marked females were made whenever they returned with a caterpillar or mudball. Wasp and caterpillar were collected and placed into a ventilated tube and unventilated tube, respectively. The caterpillar's body mass (M_{prey}) was determined to the nearest 0.001 g. Wasps returning with mudballs were also captured. Wasp and mudball were collected and placed into a ventilated tube and unventilated tube, respectively. Gentle handling of the mudballs was employed to prevent them from crumbling. The mudball's mass (M_{mud}) was determined to the nearest 0.001 g. In both situations, marked wasps were chilled, reweighed, and released as previously described. Multiple caterpillars and/or mudballs were often collected from a single individual. After a wasp arrived with its third (at most) caterpillar it was placed in an airtight tube and frozen. The number of mudballs collected before the wasp was taken was highly variable. For two individuals, both caterpillar and mudball data were obtained. Female wasps were frozen and transported to the laboratory for additional measurements. An Ohaus® analytical balance accurate to ± 0.0001 g was used to determine M_b for each female wasp. The head, abdomen, legs and wings were cut away and thorax mass (M_{th}) was measured. Because flight muscle composes 95% of thorax mass in Hymenoptera (Marden 1987), flight muscle ratio was calculated as $0.95M_{th}/M_b$. Operational (loaded) flight muscle ratio (FMR_o) was determined as $0.95M_{th}/(M_b$ + mass of load carried). Voucher specimens were deposited in the Entomology Museum of Western Illinois University.

Average M_b and unloaded FMR were calculated for individual wasps that carried multiple caterpillars and/or mudballs. The individual averages were then

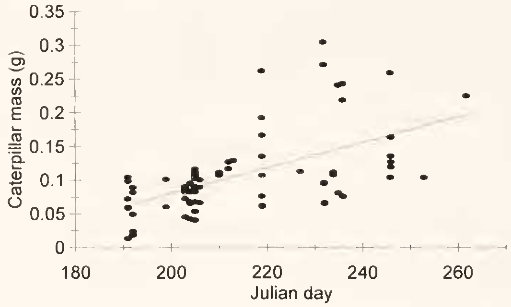

Fig. 1. The effect of time of year on body mass of caterpillars carried by *Monobia quadridens*.

used to determine all descriptive statistics for each of these categories to avoid pseudoreplication (Zar 1996). Statistical analyses were performed using Systat® 6.0 for Windows (SPSS Inc., Chicago, IL), Corel Quattro Pro® 6.02 for Windows (Corel Corp. Ltd.), and StatMost® (Datamost Corp.)

RESULTS

Data were collected on a total of 54 female *M. quadridens*: 10 from 1996, 24 from 1997 and 20 from 1998. Thirteen wasps returned more than once with loads prior to being sacrificed, thus sample sizes differ for prey, mudballs and total wasps. All prey carried by *M. quadridens* were in the family Pyralidae.

Regression analysis of M_{prey} on M_b for all wasps was not significant, nor was M_{prey} on M_{th} ($P > 0.05$). The average M_b was 0.2184 ± 0.0059, n = 54. The smallest wasp (0.09 g) was observed hauling two caterpillars simultaneously with a total prey mass of 0.104 g. This load was almost identical to the average load carried by a female nearly three times the size of the smallest wasp.

Caterpillar body mass increased over the course of the season and was linearly related to Julian day ($M_{prey} = -0.299 + 0.0019$day, n = 74, $R^2 = 0.316$, $F = 33.3$, $p < 0.0001$) (Figure 1). Late-season caterpillars were nearly double the M_b of those taken during June and July.

Increasing caterpillar size affected the

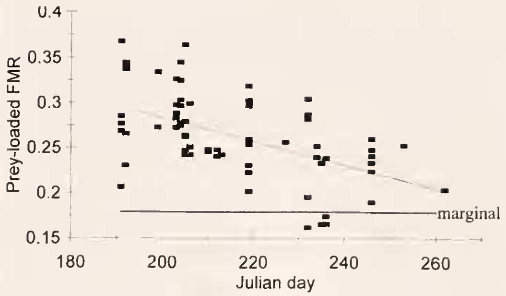

Fig. 2. The effect of time of year on operational (prey-loaded) flight muscle ratio in wasps carrying caterpillars. The marginal level indicates the minimum flight muscle ratio required for successful take-off.

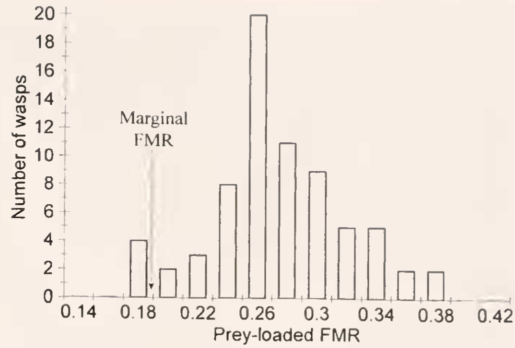

Fig. 3. The distribution of operational flight muscle ratios among wasps carrying caterpillars. The marginal level indicates the minimum flight muscle ratio required for successful take-off.

prey loaded FMR_o (0.2633 ± 0.0054, $n = 71$), which decreased significantly over the course of the season ($FMR_o = 0.544–0.0131day$, $n = 71$, $R^2 = 0.267$, $F = 25.1$, $p < 0.0001$) (Figure 2). Late in the season, the increase in prey mass caused the loaded FMRs to fall below the marginal FMR for Hymenoptera.

In four of 71 (5.6%) foraging events, the wasp had an average loaded FMR below the marginal FMR (Figure 3). Each of these individuals carried large caterpillars weighing an average of 0.252 g. This mass was 233% greater than the overall mean M_{prey} (0.108 g). No early-season, prey-laden wasp approached the marginal FMR for Hymenoptera.

As wasp size increased, the size of mudballs (mean = 0.0513 ± 0.0032 g) used during nest construction increased. Significant relationships demonstrated the effect of wasp mass on mudball mass: M_b versus M_{mud} ($M_{mud} = 0.0051 + 0.1943M_b$, $n = 38$, $R^2 = 0.270$, $F = 13.3$, $p = 0.0008$) (Figure 4). A weaker, but significant effect of M_{th} on M_{mud} was also present ($M_{mud} = -0.0054 + 0.6072M_{th}$, $n = 27$, $R^2 = 0.205$, $F = 6.44$, $p = 0.018$).

The average mudball mass was 50% less than and significantly different from ($t = 7.36$, $df = 99$, $p < 0.0001$, t-test) the average prey mass ($0.1081 \text{ g} \pm 0.0069$, $n = 74$). Consequently, the mean FMR for females loaded with mudballs, (0.3099 ± 0.0033, $n = 27$) was well above the marginal FMR.

DISCUSSION

Wasp body mass and thorax mass did not affect the size of prey provisioned. If females were actively selecting prey by size, they should take the largest caterpillars they can lift. Thus, larger wasps would be choosing larger prey, as occurs in *S. ichneumoneus* (Coelho and LaDage 1999) and *Palmodes laeviventris* Cresson (Gwynne and Dodson 1983). Females would spend less time foraging and energy would be conserved. However, observations of *M. quadridens* did not support this hypothesis.

As the season progressed, caterpillar

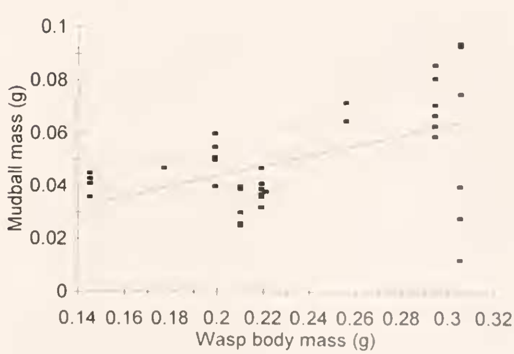

Fig. 4. The effect of wasp body mass on mass of mudballs carried by *Monobia quadridens*.

size increased, consequently decreasing the FMR_0 of foraging wasps. Early in the season, females exhibited no difficulty in carrying prey. Prey mass was never large enough to substantially decrease the FMR_0; therefore, loaded females remained well above the marginal FMR for Hymenoptera. In August, however, provisioning females encountered load-lifting constraints because of the increasingly large caterpillars. As a result, the FMR of loaded individuals dropped near or slightly below the marginal FMR.

Considering the prey cues available to predatory wasps and their acute visual abilities, it is doubtful that early in the season *M. quadridens* females would be incapable of finding larger caterpillars if such prey were present (Stamp and Wilkens 1993). It is more likely that females provisioned smaller prey at this time because they were the most readily available, if not the only suitable prey available.

In early summer, females, regardless of individual size, primarily foraged on small-bodied caterpillars. Caterpillars presumably grew as the summer progressed, and late in the season *M. quadridens* females were not always successful in their attempts to carry the larger caterpillars. On one occasion a female made no attempt to recover a large caterpillar after dropping it. Another low-flying wasp fell to the ground without dropping the prey item, crawled 30 cm up a beam then flew 183 cm (horizontal flight) and landed on a chair. Again, she tumbled to the ground and dragged the caterpillar 147 cm through the grass prior to abandoning it. These two late season caterpillars had an average mass of 0.256 g, which was twice the size of the largest early season caterpillar. As a result, individual FMR_0 fell to between 0.239 and 0.165, and caterpillars were dropped.

Typically, predators choose prey that are large enough to make it worth their time and energy, yet small enough to be easily carried (Reavey 1993). The loss of time and energy resulting from failed foraging attempts on large caterpillars suggests that either small caterpillars were in short supply, or that success was frequent enough to outweigh failure. Indeed, on occasion females successfully brought in prey larger than themselves. In one case, a female was loaded with a caterpillar 1.5 times greater than her own body mass.

Similar effects of changing prey size because of prey growth are known from other species. Seasonal variation in caterpillar size also dramatically affects the provisioning style of the solitary digger wasp *Ammophila sabulosa* L. (Field 1992). Large prey are taken more frequently during the second part of the nesting period (entire nesting period runs from late June through early September) and are carried on foot. Early in the season, when smaller prey are more common, provisioning wasps require a greater number of small prey, which they carry in flight. Furthermore, smaller wasps multiply-provision their nests (using smaller prey) more frequently than larger wasps (Field 1992).

Brockman and Grafen (1992) describe the effect of the growth of spiders on their predator, the mud-dauber, *Trypoxylon politum* Say. At the start of the season, wasps forage on a genus of spiders (*Eustala*) that overwinter as adults. The majority of the season, wasps provision with the genus *Neoscona*, which overwinter as spiderlings. As spider size gradually increases, wasps late in the season experience difficulty hauling the larger spiders, frequently dropping them. Additionally, wasps expend more energy and risk being attacked by large adult spiders. Landes et al. (1987) found that "wasps collected spiders in numbers relative to their seasonal and relative abundance, accessibility as prey, or size suitability."

In addition to carrying caterpillar prey, female *M. quadridens* also carried mudballs used in nest construction. Wasp body mass significantly influenced the mass of mudballs carried. This effect suggests that females constructed mudballs of a size proportional to their individual body size. These findings are consistent with Archer's (1977) study of *Paravespula vulgaris* (L.), in which forager body size was significantly correlated to the earthen load carried by wasps leaving the nest.

In contrast to several of the prey-loaded FMRs that dropped below the marginal FMR, females never carried mudballs large enough to substantially decrease their FMR_{mud}. The FMR_{mud} values were far greater than the marginal FMR. *M. quadridens* may not optimize energy costs of mudball production and carriage because of the style used to carry mudballs. Wasps may be restricted to making small, round mudballs compact enough to be easily carried in their mandibles. The difference in carriage style between prey and mud perhaps best explains why female *M. quadridens* could haul heavier prey loads than mudballs. Caterpillars were grasped with all legs and held lengthwise against the female's underside without altering the center of gravity (Evans 1962). In contrast, mudballs carried with the mandibles and forelegs placed additional weight toward the head, altering balance. To compensate, individuals may have been restricted to hauling mudballs that were much lighter than the prey.

On average, *M. quadridens*' unloaded FMR (0.385), although higher than the mean for Hymenoptera (0.34 ± 0.013, n = 15; data from Marden 1987, Coelho 1991, 1997, Coelho & Hoagland 1995, Coelho and LaDage 1999), is similar to that of other vespoids such as *Vespula* (Coelho and Hoagland 1995). *M. quadridens*' FMR was considerably lower than that of the ground-nesting sphecids *Sphecius speciosus* (0.416, Coelho 1997) and *Sphex ichneumoneus* (0.462, Coelho and LaDage 1999). *M. quadridens* is therefore less maneuverable than the ground nesters when unladen. However, the mass allocation of *M. quadridens* should be matched to the maximum demands of load carriage, which occur when prey are carried. Only 5.6% of provisioning events caused *M. quadridens* to have an FMR_o below marginal. In contrast, *Sphecius speciosus* and *Sphex ichneumoneus* provision at levels below marginal FMR_o 90% (Coelho 1997) and 25% (Coelho and LaDage 1999) of the time, respectively. Therefore, *M. quadridens* is on average more maneuverable when provisioning than the ground nesters. Aerial nesting may, in fact, carry maneuverability restrictions as predicted.

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